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STUDIES ON THE NATURE OF MUTATION

BY

DAVID HIRAM THOMPSON

B. S., Purdue University, 1919
M. S., University of Illinois, 1921

AN ABSTRACT OF A THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY
IN THE GRADUATE SCHOOL OF THE UNIVERSITY
OF ILLINOIS, 1924

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EVIDENCE OF STRUCTURE IN THE GENE

In the last few years the amount and variety of data concerning gene variation have reached a point where it should be possible to make a general explanation that will at least serve as a working hypothesis. An explanation of gene mutation is suggested by some recent results from the highly mutable allelomorphs of the bar series in Drosophila. These results indicate that the gene consists of a main particle, or base, firmly fixed in the chromosome, with varying numbers of other particles, or modifiers, attached to it. The modifiers of any gene are usually attached to the base in a side-chain arrangement. Mutation consists of the gain or loss of modifiers or chains of modifiers.

(1) Two cases of coincidence of mutation occurred where one full-eyed mutant and one ultrabar-eyed mutant were found among the offspring of a single bar female. The female is emphasized since other evidence indicates that almost all the mutations of the bar gene occur in the female. The male in one case was bar-eyed and in the other full-eyed. The probability that these mutants were due to independent causes is of the order of one chance in a million. Bar eye is intermediate between full eye and ultrabar eye. In these cases both extremes arose simultaneously and it seems that one of the two bar genes in a germ cell of the female had lost something and that the other gene had gained something.

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(2) The facet count of homozygous bar females is strikingly similar to that of full-ultrabar heterozygotes in those cases where the three allelomorphs of the series are derived by mutation from one stock and hence have the same titre of accessory factors. One dose of ultrabar is as effective as two doses of bar in reducing the facet number of the full eye. The difference between the full gene and the bar gene is the same as the difference between the bar gene and the ultrabar gene.

(3) The evidence indicates that one of the two bar genes of a female germ cell had lost something and that the other bar gene had gained by exactly that same amount. On the general thesis that losses can occur more readily than gains, the relative rates of mutation in the two directions should show which had lost and which had gained. Zeleny's data show that bar mutates to full about twenty times as often as it mutates to ultrabar. Therefore, the full gene is a bar gene minus something and the ultrabar gene is a bar gene plus something.

(4) This something which the bar gene may gain or lose is the *modifier* and the part to which it attaches is the *base*.

Bar mutates to ultrabar about three times in a hundred thousand flies, presumably due to the addition of a modifier subtracted from the homologous gene in a female. The full gene, however, does not add a modifier to form a bar gene so readily. Among all the millions of fruit flies so carefully examined, only one bar mutant has been found. This indicates a different order of mutation. It seems most probable that the full gene consists of a base alone and that the bar mutant arose by the addition of a modifier from some other locus.

(5) The ultrabar gene with its two modifiers mutates to full with about the same frequency as the bar gene with its one modifier. This would not be expected if both the modifiers of the ultrabar gene were attached to the base, since two breaks would have to be made as against one in the bar gene in order to attain the full condition. Therefore, it seems that the second modifier of the ultrabar gene is attached to the first modifier and not to the base. Furthermore, ultrabar mutates to full almost twice as often as it mutates to bar. This is to be expected, since pressure applied to the chain of modifiers would cause the greater strain next to the base.

(6) Sturtevant and Morgan have demonstrated that bar to full mutation is accompanied by crossing-over in that region of

the chromosome. Crossing-over is generally thought to involve intimate contact at the point of breaking. The mechanical dislocation of the modifier of the bar gene due to this intimate contact can readily be visualized.

(7) Since the facet counts of full, bar and ultrabar males resemble the facet counts of the corresponding homozygous females more than any of the heterozygotes, it is evident that the ratio of the number of modifiers to the number of bases is the potent factor determining facet number. The rate of change of facet number caused by successive additions of modifiers to the bases should give some indication of the facet number of possible allelomorphs with more modifiers than ultrabar. Excluding full since it has no modifiers, and taking the average of the counts for the bar female and the full-ultrabar heterozygote, since they have the same modifier-base ratio; the four following numbers remain in Zeleny's series: 400, 35.8, 25.7 and 22.0. The successive additions of modifiers not only cause a decrease in facet number, but the rate of decrease and the rate of the rate of decrease also become smaller. This indicates that all further additions of modifiers will give a facet count very slightly smaller than ultrabar. In effect, these allelomorphs with four or more modifiers would be completely dominant over full.

(8) A number of other measured character changes caused by mutation at the bar locus agree with the facet number data in that bar is intermediate between full and ultrabar, and that the bar female is similar to the full-ultrabar female.

(9) This explanation of the phenomena of mutation in the bar series also applies to those cases in other animals and plants in which considerable data have been accumulated. In some of these series of allelomorphs, however, there are members that can not be construed as quantitative variations of one kind of modifier, and occasionally these qualitatively different members also show a marked change in the rate of mutation. In such cases it seems that more than one kind of modifier is acting.

(10) An inspection of the chromosome maps of Drosophila shows that the loci of the various mutants are not distributed at random throughout the length of the chromosome, but are concentrated into certain regions. A comparison of these maps with the cytological figures shows that in almost every case these highly mutable regions correspond with the points of spindle fiber attachment. If these maps give a true picture of distance,

it is difficult to see why this relationship should exist unless mutation involves a mechanical alteration of the gene.

A later paper will discuss the general application of this hypothesis more fully.

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